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THE CATEGORIES OF VARIATION

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It is a well-established fact that what are commonly called variations include modifications of quite different import in relation to the process of evolution. Whether or not the variations that are induced in the soma, either by its own activities or through the influences of the environment, have any effect in shaping the course of evolution as they were held to do by Lamarck and his followers, it is evident that they do not count in this process in the same way as variations that arise in the germ. But among the germinal variations themselves there are classes of unequal significance. Variations differ markedly in regard to their stability or permanence. Many variations after their first appearance persist with little modification for an apparently indefinite time. Of these what are commonly called mutations afford conspicuous examples; these are abrupt variations which breed true or nearly so from the start, having their own fluctuating variability, to be sure, but around a mean which does not approach that of the parental type in successive generations. Other variations behave quite differently. They may be selected generation after generation, modifying the stock up to a certain point, after which, if the variety is left to itself, there is revision towards the original parent. It is held by many that these two classes of variations are fundamentally distinct, and that only the first,

so-called discontinuous variations, play an important rôle in the origination of new species.

A considerable proportion of what is described as fluctuating variability is, in many cases, simply somatic variation, having no relation to the germ plasm. It is evident, however, that all fluctuating variability can not be such, otherwise species could not be modified by ordinary methods of continued selection. Our mathematical curves represent two kinds of variability lumped together and which it is in most cases practically impossible to separate. The character of height, for instance, in human beings is to a certain extent an inherited one, but it is determined to a marked degree by influences operating after birth. The usual curves of variation represent both and may even include also variations in the nature of mutations which fail of discrimination from the rest of the aggregate.

De Vries distinguished three kinds of germinal variations, elementary species, retrograde varieties and fluctuations. These three kinds he conceives to be sharply distinguished and produced in different ways. All congenital variability is regarded by him as resting upon qualitative or quantitative changes in the pangens or the organic units of which he conceives living matter to be built up. The pangens form the basis of the unit characters, or independently variable elements of the organism, there being a special kind of pangen for each such character. Variations in the number of pangens cause variations of the fluctuating type which obey Quetelet's law of chance frequency distribution. De Vries maintains and attempts to prove by the citation of several examples that through the selection of such variations modification may be carried to a certain point, but soon a limit is reached beyond which selection is incompetent to effect further improvement. Moreover, continued selection must be practised in order to maintain the condition which has been reached, else the stock will in the course of a few generations revert more or less completely to the ancestral mean.

Retrograde varieties, according to De Vries, are sharply distinguished from fluctuations. They are, as a rule, constant from the start, and differ from the type in only one or at most a very few respects.

They originate for the greater part in a negative way by the apparent loss of some quality and rarely in a positive manner by acquiring a character seen in allied species." "By far the greatest part of the ordinary garden-varieties differ from their species by a single sharp character only. In derivative cases, three or even more such characters may be combined in one variety, for instance, a dwarfed variety of the larkspur may at the same time bear white flowers or even double white flowers, but the individuality of the single characters is not in the least obscured by such combinations.

These varieties, says De Vries, "do not possess anything really new." The loss of a character is merely apparent. "On a closer inquiry we are led to the assumption of a latent or dormant state. The presumably lost characters have not absolutely, or at least not permanently disappeared. They show their presence by some slight indication of the quality they represent, or by occasional reversions. They are not wanting, but only latent." In other words, the only difference between retrograde varieties and the types is the latency or patency of certain characters. The same kinds of pangens are present in the germ plasm of both.

Elementary species, on the other hand,

are distinguished from their nearest allies in almost all organs. There is no prominent distinctive feature between the single forms of *Draba verna*, *Helianthemum* or of *Taraxacum*; all characters are almost equally concerned. The elementary species of *Draba* are characterized, as we have seen, by the forms and the hairiness of the leaves, the number and height of the flower stalks, the breadth and incision of the petals, the forms of the fruits, and so on. Every one of the two hundred forms included in this collective species has its own type, which it is impossible to express by a single term. Their names are chosen arbitrarily. Quite the contrary is the case with most of the varieties, for which one word ordinarily suffices to express the whole difference.

The most important distinction which De Vries draws between retrograde varieties and elementary species is a physiological one. They

behave in quite different manner, when subjected to crossing experiments, and the hope is justified that some day crosses may become the means of deciding, in any given instance, what is to be called species, and what variety on physiological grounds.

When varieties are crossed with the parent type the character that is active in one or the other of the forms will usually be patent in the first generation of offspring. In the second generation there is, according to De Vries, a segregation of characters which takes place in conformity to Mendel's law. Ordinary sugar corn, for example, differs from the usual type in having a part of the starch replaced by sugar in the kernels, which consequently become wrinkled when dry. When these two forms are crossed the active character of starchy kernels is present in all the members of the first generation. In the second generation there is a segregation of these characters, one fourth of the offspring being wrinkled kernels, and three fourths smooth ones. Approximately one third of the latter produce only smooth kernels in subsequent generations, while the other two thirds split up again in the expected Mendelian ratio.

In the crossing of varieties it is possible, according to De Vries, for all the corresponding characters of the two forms to become paired. As the distinguishing feature of the variety is the latency or patency of one or more characters, these characters "will unite as well as though they were both active or both dormant. For essentially they are the same, only differing in their degree of activity. From this we can infer that, in the crossing of varieties, no unpaired remainder is left, all units combining in pairs exactly as in ordinary fertilization." As the varieties differ only in the dominance or latency of certain characters, offspring obtained through crossing them differ only in the same way. For such unions De Vries gives the name "bisexual crosses," inasmuch as there is "complete bisexuality, all unit characters combining in pairs."

In the crossing of the elementary species of *Oenothera* De Vries found that in the first generation there was a

splitting up of the progeny in various ratios, but that the second and subsequent generations bred true to type, thus presenting a condition just the reverse of Mendelian inheritance. For instance when the mutant *rubrinervis* was crossed with the parent type *Lamarckiana* the first generation of hybrids were either *rubrinervis* or *Lamarckianas*, the proportion varying greatly in different lots. The two kinds of hybrids did not split up in the second generation but bred true to type. Similar results were obtained by crossing several other elementary species of *Lamarckiana* but this kind of behavior does not seem to be generally characteristic of the elementary species of other forms.

In the crossing of elementary species there is, according to De Vries, one unit character which is not mated, since

the differentiating mark is present in one of the parents and not in the other. While all other units are paired in the hybrid it is not. It meets with no mate and must therefore remain unpaired. The hybrid of two such elementary species is in some way incomplete and unnatural. In the ordinary course of things all individuals derive their qualities from both parents; for each single mark they possess at least two units. Practically but not absolutely equal, these two opponents always work together and give to the offspring a likeness to both parents. No unpaired qualities occur in normal offspring; these constitute the essential features of the hybrids of species and are at the same time the cause of their wide deviations from ordinary rules.

These differences between variations were predicted by De Vries on the basis of his pangen theory, and in his essay on "Intracellular Pangenesis" published in 1889 he expresses the opinion that fluctuating variability which rests upon numerical variation of the pangens plays but a minor part in the modification of species. The "art-bildende" or species forming variability, is dependent upon the appearance of an entirely new kind of pangen. When categories of variation are anticipated *a priori* on the basis of a theory of the constitution of living matter there is naturally produced a temptation or bias towards

reading the classification into nature and to the overlooking of transitional stages, and we shall therefore enquire if the distinction which is made between elementary species and varieties is a valid one.

In the first place, there does not seem to be any very good reason why on the pangen theory elementary species should differ in numerous characters from the parent form. A pangen is the basis of a single unit character. Elementary species are produced through the origination of a new kind of pangen. If the becoming latent or dominant of a pangen affects only one unit character of an organism, it is not evident, when a new kind of pangen is produced, why the whole organization of the plant should be so profoundly influenced. Why should not the awakening of a dormant pangen produce as great a change as the production of a new pangen of a somewhat different quality. Says De Vries:

There can be little doubt but that all the attributes of every new species are derived from one principal change. But why this should affect the foliage in one manner, the flowers in another and the fruits in a third direction, remains obscure. To gain ever so little insight into the nature of these changes, we may best compare the differences of our evening primroses with those between the two hundred elementary species of *Draba* and other similar instances. In doing so we find the same main feature: the minute differences in nearly all points.

De Vries nowhere gives us a much clearer explanation as to why elementary species and varieties should differ in this way and we must probably be content with referring the matter to different degrees of "correlation."

It is evident that there are allied groups separated by small differences throughout the entire organization, and there are other groups which differ apparently in single characters only, such as the presence or absence of hair, spines or certain colors. Hornless cattle and six-toed cats do not seem to present any general or constitutional differences from the other members of their species, but this is a subject upon which we should exercise great caution, as very slight differences in the rest of the organ-

ization may be correlated with pronounced differences in a single part.

Among the forms arising by mutation from *Oenothera lamarckiana* De Vries distinguishes three varieties, *lævifolia*, *brevistylis* and *nanella*. These forms are called varieties instead of elementary species because they differ from the type in a few characters only and because of their different behavior when crossed. But even according to De Vries' own description the points of difference are not limited to a single character. *Lævifolia*, for instance, is

chiefly distinguished from Lamarek's evening primrose by its smooth leaves, as its name indicates. The leaves of the original form show numerous sinuosities in the blades, not at the edge, but anywhere between the veins. The blade shows numbers of convexities on either surface, the whole under surface being undulated in this manner. It lacks the brightness of the ordinary evening-primrose or *Oenothera biennis*. These undulations are lacking or at least very rare on the leaves of the new *lævifolia*. Ordinarily they are wholly wanting, but at times single leaves with slight manifestations of this character may make their appearance. They warn us that the capacity for such sinuosities is not wholly lost, but only lies dormant in the new variety.

The leaves of *lævifolia* are also "a little narrower and more slender than those of the *Lamarckiana*." But *lævifolia* also shows differences in the flower. "The yellow color is paler and the petals are smoother. Later in the fall, on the weaker side branches these differences increase. The *lævifolia* petals become smaller and are devoid of the emargination at the apex, becoming ovate instead of obcordate."

Brevistylis is characterized by its short style. The stigma is different in shape from that of the parent form; there are differences in the ovaries, and there are only a few seeds produced. These differences may possibly depend upon a single varying character, although

the leaves of the *O. brevistylis* are more rounded at the tip, but the difference is only pronounced at times slightly in the adult rosettes, but more clearly on the growing summit of the stems and branches. By this character the plants may be discerned among the others, some weeks before the flowers begin to show themselves.

Nanella is a dwarf plant, but it is not distinguished by its smaller size alone.

From its first leaves to the rosette period, and through this to the lengthening stem, the dwarfs are easily distinguished from any other of its congeners. The most remarkable feature is the shape of the leaves. They are broader and shorter, and especially at the base they are broadened in such a way as to become apparently sessile. The stalk is very brittle, and any rough treatment may cause the leaves to break off. . . . The stems are often quite unbranched, or branched only at the base of the spike. Strong secondary stems are a striking attribute of the *Lamarckiana* parent, but they are lacking, or almost so in the dwarfs.

So far as morphological evidence is concerned, the difference between the above forms and elementary species are not so sharp as to inspire one with much confidence in the essential distinctiveness of the two classes. All of these so-called varieties differ in various parts of their organization. It may be said that these differences are dependent through correlation upon the variation of a single character, but if any one maintains that smooth leaves and paler flowers, or small size, brittle stem and short leaf stalks are related in this way, the burden of proof is on his shoulders. If a half dozen characters in different parts of the plant vary it would indeed be difficult, amid a considerable amount of fluctuating variability, to separate on morphological grounds a retrograde variety from a true elementary species, especially since experts are sometimes troubled in distinguishing some of the elementary species from one another. Indeed, De Vries admits that it is often very difficult to decide whether a given form belongs to one or the other of these two groups, but he states that in such cases we have a means of testing the matter experimentally by the formation of crosses. Let us see, therefore, how the test of crossing works out.

In the case of the varieties of *Oenothera lamarckiana* there is in the second generation a splitting according to the Mendelian ratio when the variety is crossed with the parent form, but with varieties of other forms this does

not seem to be an invariable occurrence. Davenport has shown that albinism in poultry is in some cases a non-Mendelian character, and the same is probably true, according to Castle, for the lop-eared condition in rabbits. In the inheritance of long and short hair in guinea pigs there is also a marked departure from Mendelian ratios. In silkworms Kellogg has shown that while most features are Mendelian, cocoon color in some cases follows Mendelian ratios, but in others it proved to be "inconstant as to dominance and recessiveness and numerical proportions, and may even break down and blend." Deaf-mutism also refuses to come under Mendelian categories according to the statistics compiled by Bell. The foregoing are cases of apparent retrograde variations which form an exception to Mendel's law, but it must be admitted that the majority of such variations which have been investigated show a fair approximation to Mendelian ratios.

In the crosses between the elementary species of *Oenothera lamarckiana* there is commonly a splitting up in the first generation with absence of splitting in the second and subsequent ones. Hybrids of *O. Lamarckiana* and *O. biennis*, however, have nearly the aspect of the latter species and remain true in the second and subsequent generations without reversion or splitting. Crosses between *O. muricata* and *O. lutea* produced hybrids showing the characters of both parents. These were propagated through four generations and remained "true to this type, showing only slight fluctuations and never reverting or segregating the mixed characters." Instances of constant hybrids between different species are very common and it is unnecessary to specify them here. Such constancy according to De Vries is "one of the best proofs of unisexual unions" or unions between distinct elementary species in which there is always one unpaired pangen.

The attempt to make a general rule for the hybridizing of elementary species leads to many difficulties. In

poultry, as Davenport has pointed out, such characters as pea and rose comb, extra toes and the presence of muffs and beards on the head, are acquisitions which developed since the domestication of the original ancestral species. They certainly can not be regarded as the outcropping of latent characters which are represented in allied forms, but are in the line of progressive variation and therefore according to theory dependent upon the production of new kinds of pangens. any definite rule of inheritance and none of them follow Mendel's law, the extra toes do not seem to come under any definite rule of inheritance, and none of them follow the rule for the hybridization of elementary species.

Consider the forms of the common potato beetle studied by Tower. These arise suddenly, breed true to type and differ from the parent form in many characters, some of which are apparently in the line of progressive evolution. They seem to be as truly elementary species as the mutants of *Oenothera lamarckiana*. Yet when crossed with the parental type they produce hybrids which in most cases give a mixed progeny segregating according to Mendel's law. If we can not call these forms elementary species there is no way of distinguishing such except through breeding experiments, and the distinction De Vries draws between elementary species and varieties amounts to nothing more than the fact that crosses between certain groups follow Mendel's law, while crosses between others do not. There is no correlation between any structural criterion of species and the criterion afforded by breeding experiments.

Now when we attempt to make a classification on the basis of breeding experiments alone we fare little better. With blended inheritance in the first and all subsequent generations, partially blended inheritance, total resemblance of hybrid to one or another parent with or without subsequent splitting, incomplete segregation of characters, splitting of offspring of hybrids in various inconstant and non-Mendelian ratios, and many other irregular

manifestations of heredity, the difficulty of maintaining a sharp distinction between varieties and elementary species on the basis of behavior in inheritance is apparent. Are we to classify a six-toed cat as a variety or an elementary species? The variation is apparently limited to a single character and it has therefore one of the marks of a variety, but the variation is doubtless a progressive one and not due to an awakening of a latent character, and hence possesses one of the features of an elementary species. When crossed some of the offspring of the first generation may inherit the variation and some not, and the same is true for the following generation; but there is apparently no splitting according to the law of Mendel. So far as our knowledge goes the situation is the same in respect to polydactylism in man.

The second volume of the *Mutationstheorie*, which seems to have been little read by most expositors of De Vries, affords several examples of irregular behavior of the hybrids between elementary species which are very difficult to classify. Crosses between *Oenothera nanella* and *O. rubrinervis*, for instance, the one a retrograde variety of *Lamarckiana* and the other a distinct elementary species, gave very variable results, with splittings in the first and succeeding generations in very inconstant ratios, and the occasional production of blends which bred fairly true. We have here a curious combination of the characteristics of unisexual and bisexual crosses.

It would not be difficult to bring forward many other cases which refuse to fall within the scheme of classification propounded by De Vries. There are many kinds of variations which are inherited in many kinds of ways. The pangen theory of the celebrated botanist has proved a deceptive guide and has led its author to do scant justice to many classes of facts which do not fall in line with it. Hypotheses about paired and unpaired pangens have determined De Vries's classification of the different kinds of variations and profoundly influenced his interpretation of his extensive and valuable researches. The doctrine

of intracellular pangenesis has never received the logical development that characterizes Weismann's theory of the germ plasm and is considerably inferior to the latter as a scholastic production. The explanation it affords of the alleged distinction between varieties and elementary species is, as we have seen, practically no explanation at all. The theory may be consistent with the facts of Mendelian inheritance and the supposed independent variability of parts, but why it should lead one to anticipate that elementary species differing from the parent throughout their organization originate by a single sudden leap is not so clear. Rather it would lead one to expect that organisms would be modified, a part here and a part there, corresponding to the independently variable elements determined by particular pangens, of which there are numerous kinds, until the whole was slowly transformed. De Vries, however, is careful to explain that a single pangon may be responsible for certain characters found in various parts of the organism, such as the color of leaves, flower and fruit, and that pangens are supposed to influence each other's manifestation so that a variation in a single pangon may have a far-reaching effect. In a chapter on the association of characters in his recent book on Plant Breeding a great deal of emphasis is laid upon the value of a study of the correlation of the different parts of the plant. He says:

We come to the conception of a general interdependency of all parts, organs and qualities of an organism. They are governed more or less by the same laws which cause them to undergo corresponding changes when subjected to the same influences.

It seems to me that the author is here upon treacherous ground. Through the assumption of manifold correlations De Vries attempts to account for a change in a single pangon which has to do primarily with one independently variable part of the organism producing a modification of the organism as a whole, but in so doing he is taking the foundation away from the argument upon which the justification of the pangon assumption rests.

To the extent that the organism is a whole of interdependent parts, to just that extent it gives evidence of not being a piece of mosaic work and hence removes the necessity for a hypothesis of discrete germinal units. De Vries even goes so far as to say that "in order to be correlated the characters must begin by being independent entities which through some later means may come into relation with others." At one time it is argued that the existence of pangens is proved by the fact that the parts of the organism are independently variable; and now it is said that we must assume that pangens must exist to account for the parts being correlated; that is, for the fact that they are not independently variable!

The most salient feature of the mutation theory is that the process of evolution is conceived to take place by sudden steps of considerable magnitude. This has been heralded with *éclat* as enabling us to get rid of certain difficulties inherent in the Darwinian theory, such as the assumed absence of intermediate forms between existing and fossil species and even the contention that the geological history does not afford time enough for the process of evolution as it was formerly conceived to take place. But it is not correct to say that a mutation is necessarily a large variation. Mutations may be very small steps, falling far within the limits of ordinary fluctuating variability, as is especially emphasized by De Vries in his later writings.

In groups (such as brambles, roses, buttercups, willows and many others) where large numbers of species are closely allied, the differences between any two of them become smaller, and the number of distinct forms increasing, the distinction in the end may become reduced to a single differential mark for each two neighboring types. Such differences must be assumed to be produced each by a single mutation.

In the light of experiments made at Svalof, De Vries now concludes that "ordinary varieties of cereals are built up of hundreds of elementary forms which with few exceptions have hitherto escaped observation. The high variability which is commonly attributed to our ordinary

varieties of cereals consists only in the differences among the constituents of the mixtures." Much of the improvement of grains that was formerly obtained by continued selection De Vries ascribes to the unconscious selection of elementary species and the gradual improvement of an originally mixed stock. Rimpau's rye, a stable race obtained by gradual selection, is thus accounted for, but the burden of proof is here on the part of the mutationists. It is apparently not so easy to test the rôle of mutations *versus* fluctuations in the improvement of species, because if one should secure a stable race by the usual process of selection, the mutationist might urge that, after all, amid the confusion of seemingly fluctuating variability, there were some mutations which escaped notice, and, through the unconscious selection of these and their offspring, the stock was gradually purified and converted into an improved stable form.

Where ordinary varieties include "hundreds of elementary forms," separated by characters which in many cases are so small that they "may be scarcely perceptible to the inexperienced eye," how is one to tell whether he is dealing with mutations or ordinary fluctuations? The latter may be much greater in extent, and, as we have seen, there is no structural criterion by which a mutation may be recognized. Crossing experiments give us no certain test and we have therefore to fall back upon the criterion of stability and class as mutations those variations which breed true from their first appearance. Here the opportunities for begging the question are excellent. If by the ordinary process of selection a stable race is produced we can of course ascribe it to the unconscious choice of one or more undetected mutations. To be sure, stable races can be produced only on the basis of stable variations, and if this is all that the mutation theory necessarily implies its divergence from Darwin's teaching is not very wide.

If now it should turn out that stability is a matter of degree the last distinguishing feature of the mutation

theory would be destroyed. This is a question upon which we are sadly in need of light. Some of De Vries's own mutations are, however, quite inconstant and show a strong tendency to revert to the parent species. *Oenothera scintillans*, when self-pollinated, produced from 8 per cent. to 52.9 per cent. of *Lamarckianas* and 34 per cent. to 69 per cent. of its own kind and a variable number of other mutants. *O. elliptica* and *O. linearis* repeat their kind in still smaller ratios. The reversion of these mutants like their origin is sudden, but it shows an unstable condition of their germ plasm and it may be questioned if this reversion is essentially different from the slower reversion which often follows the cessation of the selection of ordinary fluctuations.

That the differences between mutations and fluctuations are not so fundamental as the pangen theory implies is indicated by several facts, some of the most suggestive of which have been furnished by De Vries's own experiments. For a number of years De Vries carried on a series of experiments on the corn-marigold *Chrysanthemum segetum*, with the purpose of creating a double-flowered variety. De Vries chose a garden variety of this form, *grandiflorum*, and raised several generations, selecting the seed each time from heads which contained 13 rays florets. After four years of propagation, when he was satisfied of the purity of the isolated strain, De Vries began to discard all plants with less than 21 rays in the terminal head. The selection was continued for a number of generations when a plant appeared which seemed to form a promising one for the production of a double variety.

It was not remarkable for its terminal head, which exhibited the average number of rays of the 21-rayed race. Nor was it distinguished by the average figure for all the heads. It was only selected because it was the one plant which had some secondary heads with one ray more than all the others. This indication was very slight, and could not have been detected save by the counting of the rays of thousands of heads. But the rarity of the anomaly was exactly the indication wanted, and the same deviation would have had no significance what-

ever had it occurred in a group fluctuating symmetrically around the average figure. On the other hand, the observed anomaly was only an indication, and no guarantee of future developments.

From this slight indication De Vries selected for three years more and found that the

average number of rays increased rapidly and with it the maximum of the whole strain. The average came up from 21 to 34. . . . The largest numbers determined in the succeeding generations increased by leaps from 21 to 34 in the first year, and thence to 48 and 66 in the two succeeding summers.

Up to this time, while there was a great increase in the number of ray florets, there was no trace of doubling, but in a few of the best heads "the new character suddenly made its appearance." If sudden, the step was certainly a very modest one. A single plant was found in which careful inspection revealed "three young heads with some few rays in the midst of the disk." "Had the germ of the mutation," asks De Vries, "lain hidden through all this time? Had it been present, though dormant, in the original sample seed? Or had an entirely new creation taken place during my continuous endeavors? Perhaps as their more or less immediate result?" It is stated that "The new variety came into existence at once"—but when? While certain that a mutation must have appeared, De Vries is uncertain when and where it appeared. "The leap," he says, "may have been made by the ancestor of the year 1895, or by the plant of 1899 which showed the first central rays, or *the sport may have been gradually built up during these four years*" (italics mine).

During the next two years improvement by selection was kept up.

The average number of rays which had already risen from 13 to 34 now at once came up to 47 and 55. . . . The maximum numbers came as high as 100 in 1900 and even 200 in 1901. . . . Real atavists or real reversionists are seen no more after the first purification of the race.

A variety which is pronounced "permanent and constant" was produced whose lower limit of the number

of rays was raised to about 34, "a figure never reached by the *grandiflora* parent."

The unbiased reader who has carefully followed the account of the production of this double flower can scarcely escape the feeling that the interpretation of the facts according to the mutation theory is at times somewhat strained. The starting point of the whole process is the selection of fluctuations. Now and then the selection of a somewhat more pronounced variation was made; but the so-called mutations had very small and weak beginnings, and De Vries is uncertain just where they occurred and even suggests that they may have been built up gradually! The selection of fluctuations seems to have had the effect of inducing variations of greater stability, if not greater extent, in the same direction. It is not unreasonable to suppose that the appearance of florets with ligulate corolla on the disk is due to the same factors which cause the increase in the number of ray florets, and the variation may be in reality not so discontinuous as it seems. In fact we are ignorant of the stability or the real discontinuity of many of the steps in advance towards the production of the double flower. If a mutation can make its appearance as an extra ray floret in one case, and by the occurrence of two or three ligulate corollas on the disk of a few flowers of the plant in another, and if both these characters can be increased by selection until they reach a stable condition that is far more highly developed than their original one, the facts do not lend much support to a theory of the saltatory origin of species. Rather they would indicate that species have been formed along lines determined by selective processes much in the same way as Darwin conceived them to be.

By a similar method of selection Burbank has produced a scarlet variety of the California poppy, *Eschscholtzia californica*. He noticed one flower with a fine scarlet line on one petal. From the seed of this plant other poppies with scarlet lines were produced, but only to a slight extent. After selection was practised for some years

a race of pure scarlet poppies was finally obtained with no indication of their yellow ancestor. This case is cited by De Vries as one of mutation, but certainly it required more than one mutation to bring about the result.¹

Discontinuity may often be more apparent than real, the discontinuous variations in the soma being the outcome of continuous variability instead of abrupt changes in the germ. Let us consider from this point of view the occurrence of digital anomalies such as polydactylism, cleft hand, etc., which are frequently cited as illustrations of discontinuous variability. These anomalies are often strongly inherited, but in most cases which have been fully studied, the inheritance, while partly alternative, is not Mendelian. In the race of polydactylous guinea pigs which Castle has produced and bred for a number of generations the anomaly appeared in different individuals in various stages of completeness. The parent of the group, a male, bore an imperfectly developed toe on his left hind foot. The extra toe contained a claw and probably the phalanges, but it was loosely attached and hung limply down on one side. This male produced 27 young, of which 15 were polydactylous. Of the latter some had an extra digit on both hind feet, others had it on but one, and in a few individuals the digit was more fully developed than in the father. In subsequent generations the anomaly appeared in very different degrees of development, some animals having a fully developed digit, others having a loosely hanging toe with or without a nail, while in extreme cases there was only a fleshy bag of skin without bones or claw which often shriveled up and disappeared a few days after birth. The variation, when appearing on one side alone more frequently was limited to the left side (l. 630, r. 589), and when unequal on the two sides the left one was usually the better developed. Normal and polydactylous individuals did not segregate in Mendelian ratios. In some instances the normal condi-

¹ See also the experiments of MacCurdy and Castle in relation of continuous and discontinuous variation in rats. Publications of the Carnegie Institution, No. 70, 1907.

tion gave evidence of being recessive, but this was not borne out by many other cases in which crosses between normal individuals produced polydactylous young. Crosses of normal individuals both of which were of polydactylous ancestry yielded a much higher per cent. of polydactylous young than did crosses in which one individual came from a normal breed, thus showing a certain tendency in the blood towards polydactylism even when it did not manifest itself by any outward mark. Different males of the same amount of polydactylous ancestry often showed great variation in the potency with which they were able to transmit the anomalous character.

The evidence goes to show that we are dealing here with a tendency which, whatever may be its basis, varies continuously and not abruptly, although producing variations which, taken alone, would naturally be classed as mutations. The extra toe is a new character, but the polydactylous breed behaves neither like an elementary species nor like a retrograde variety. The character fluctuates to the vanishing point and even beyond (as shown by crossing experiments with individuals of different ancestry) and shows varying degrees of fidelity of transmission in different strains. Do we not have a condition intermediate between the abrupt discontinuous variations which breed true with great fidelity and ordinary fluctuations? It might be said that we have to do with a mutation which fluctuates to an unusual degree, although it originally depended upon a sudden change in the germ plasm; but the assertion would have no evidence to rest upon. It might be said, on the other hand, that the variation is dependent on the undue activity of some of the factors of normal development, an expression, for instance of increased growth tendency in the part at a certain period, and that this tendency is kept from definite expression until it reaches a certain strength, when it manifests itself as a sudden variation. This conclusion is warranted, I believe, not only by the great variability

of the anomaly, but by the fact already cited that normal individuals of abnormal ancestry are more apt to produce abnormal offspring than are normal individuals of another strain.

The studies of Lewis and Embleton and of Pearson on the inheritance of split hand and split foot in man yield results in many respects similar to the preceding. Although the normal condition seems to be recessive, segregation does not occur in Mendelian ratios. Often both hands and both feet were abnormal, but frequently not in the same way, and in many cases there were marked differences in the variations on the two sides of the body. As Pearson remarks, it is difficult to specify in such cases what the unit character may be. With this, that or the other bone present in some individuals and absent in others and represented in very varying degrees of development, the inheritance gives little evidence of definite units of any kind. What is inherited appears to be a condition which manifests itself in varying ways and degrees and which can not be accounted for by any theory of the sharp segregation of characters.

Why certain germinal variations are strongly inherited and others not is a problem of much interest, but the solution of it may lie, not in the supposed behavior of distinct morphological entities representing certain parts, but in the physiological relations of the basis of the variation to the organized structure of the germ plasm. The sex cells are organisms as well as the bodies that arise from them; they have the same capacity for self regulation; and it is not at all probable that all kinds of variations that may arise in response to the various influences to which they are subjected should be retained to the same degree. Weismann has made the suggestive comparison between the variations of an organism and the oscillations of a polyhedron on one of the faces upon which it rests. If the oscillations are small the body tends to come to rest in the same situation as before; if they are larger it may topple over upon a new face about which it may oscil-

late as around a new center of equilibrium. Weismann postulates a self-regulating power in the germ plasm which keeps numerous minor fluctuating variations from producing any essential modification of the stock. If, however, a certain variation forms a new center of stability it may be permanent. The various mutants of *Oenothera lamarckiana*,² most if not all of which contain the potency of giving rise to any of the others and which present very different degrees of stability, may be due to more or less stable forms which the germ plasm may assume rather than the creation of new kinds of germinal units. The stability of a variation may be due, however, not so much to its extent as the analogy with the polyhedron might lead us to expect as to its kind. Variations which are physiologically congruent with the organized structure of the germ plasm form stable races; those which are not tend to become reduced sooner or later to the norm through the regulatory activity of this substance.

The germ plasm may be conceived to exercise, in regard to its variations, a kind of selective activity which may manifest itself as a proneness of the organism to vary along certain lines. It is well known that there are particular types of variation which crop out independently and more or less frequently and may be faithfully perpetuated. Polydactylism, split-hand and split-foot, albinism and melanism, the appearance of races of hairless animals and glabrous plants, the development of nectarines from peaches and peaches from nectarines, the origin of peloric flowers, etc., have occurred many times in independent

² It is of course possible that the mutations of *Oenothera Lamarckiana* result from the impurity of the stock. The species has been for a long time cultivated as an ornamental flower, and we have nothing but conjecture regarding its origin. Should it turn out to be derived from a mixture of two or more forms the mutation theory would be deprived of some of its best evidence, but there would still remain a considerable number of mutations from pure ancestry. In *Oenothera gigas* the interesting fact has been discovered that there is double the normal number of chromosomes. Whether this is the cause or the effect or merely one instance of the differences between this mutant and the type is unknown.

strains. These phenomena may be compared to various anomalies which take their origin in the soma. The embryo in its development is liable to certain accidents resulting in the production of teratological phenomena such as hare-lip, double formations, anencephaly and many others. These anomalies fall into certain classes and in many cases can be attributed to particular defects of development. The germ plasm also may be regarded as liable to certain classes of accidental modifications which produce heritable variations of more or less clearly defined types. No one would think of attributing anomalies of somatic origin to the development of a new kind of organic unit. If the same mutation appears time after time, would it not be more reasonable to suppose that it arose after the fashion of somatic anomalies than that it depended upon the creation each time of the same kind of a new pangen? The fact that mutations can be induced through the influence of the environment certainly favors such a view. Tower found that in *Leptinotarsa* certain variations or mutations arose repeatedly in independent strains and that by subjecting the beetles to unusual conditions during the period of active development of their germ cells the proportion of these sudden variations could be very greatly increased. The variations thus produced belonged to a few well-marked types, and while it would be hazardous to set bounds to the possible number of mutants the species may produce, it is probable that the number is subjected to a certain limitation imposed by the peculiar organization of the germinal substance.

The selection of variations by the germ plasm may be illustrated by some observations of Jennings upon inheritance in Protozoa. In a few specimens of *Paramœcium* it was noticed that the body was furnished with a spine-like excrescence. During fission the spine was transmitted to but one of the individuals, the acquired peculiarity not arising on the other. In one case the spine was transmitted through twenty-one generations, when the

strain disappeared. In other cases the spine was gradually diminished during successive divisions and ultimately disappeared. Other anomalies such as crookedness, blunt ends, bent tip of body and various abnormalities, provoked by artificial mutilation, while persisting for a variable number of generations, were eventually regulated out, leaving a normal strain.

In like manner we may imagine that through environmental changes the germ plasm becomes affected by modifications which in the course of a few generations become regulated out, thereby causing a reversion to the primitive stock. Reversion may thus be conceived as but a manifestation of form regulation. Variations to be permanent must be accepted by the organized structure of the germ cells, so that they may be included instead of excluded by the processes of functional equilibration to which these cells like other parts of the organism are continually subjected. The congruity of the variation is the important thing; whether the variation be large or small, sudden or slow, is of much less consequence.

After all, it may be asked, granting that variations may be interpreted in the manner here set forth, do not the phenomena of Mendelian inheritance, showing as they do that characters may be separated and combined in many different ways prove that these characters must be borne by some sort of units in the germ plasm? This is a conclusion which is adopted by a large number of Mendelians, but, plausible as it seems, it is, I believe, a totally erroneous view. In the first place it is open to question if the assumed purity of the gametes is a fact even in typical cases of Mendelian inheritance, but, granting that there is an absolute separation of ancestral tendencies, it by no means follows that there is any sorting of individual unit characters apart from the complex of tendencies which make for the production of the organism as a whole. Hereditary anlagen may perhaps be shuffled and sorted as wholes, but if the germ plasm were composed of discrete parts representing the unit characters

of the individuals, the result would probably be utter confusion instead of orderly development. We might assume that albinism is dependent upon the peculiar properties of a single chromosome, that length of hair is dependent upon the constitution of a second chromosome, that a short tail is associated with a third, and so on. These characters may not be represented by any kind of structural element; they may have their basis in the general chemical constitution of the chromosome and be produced during development in a purely epigenetic fashion. Chromosomes probably have their individual peculiarities of chemical constitution as might be expected from the fact that the chromatin content of an individual represents contributions from many different ancestors. Each chromosome or even a small constituent of the chromosome may have a relation to the inheritance of the whole body, but the peculiarities of one chromatic element may dominate in one part, those of another chromatic element in another. When albinism is eliminated it does not mean that this character alone is separated, but *the anlage of an albino organism*. Even if it is shown that the number of separate characters which Mendelize is greater than the number of chromosomes of the variety, Mendelian phenomena can be explained on the basis of sorting out ancestral tendencies as wholes instead of unit characters. The facts of Mendelian inheritance at present known do not necessarily give any support to the theory of discrete bearers of unit characters, or the theory of the independent variability of parts as conceived by De Vries and Weismann. This is a point which, I believe, needs to be emphasized on account of the uncritical acceptance of these views by so many writers on heredity and variation. The presence or absence of certain characters may be independent of the presence or absence of certain others, but this fact may very readily be accounted for without having recourse to a particulate theory of inheritance.

The mixing up and separation of characters in inheritance, far from proving the independent variability of

parts, is just what renders the proof of this theory exceedingly difficult. The alleged independent variability of parts is Weismann's strongest proof of his doctrine of determinants. If a pit in the ear or a white tuft of hair on the head can be transmitted for several generations without involving any other change in the organism, we are forced to assume, according to Weismann, that there is a small part of the germ plasm varying independently of the rest which forms the basis or determinant of this character. But the contention particularly difficult of proof is that the characters really do appear in independence of the other parts of the organism. A variation may conceivably depend upon a general change in the constitution of the substance of heredity, although manifesting itself most conspicuously in a single part. A pit in the ear may be the most obvious sign of the very slight constitutional differences between two individuals. It is common to find two closely allied species or varieties differing markedly in one or two features and much less conspicuously in numerous other parts of their structure. Peculiarities of horns are sometimes associated with less noticeable characteristics of the hair, thus pointing to a common origin of these features in some general modification of the ectoderm which in turn may result from some change affecting the germ plasm as a whole. Albinism which is so often cited as a unit character is a peculiarity of far reaching correlations, being often associated with impaired sight or hearing, diminished fertility, and even lessened power of resistance to disease.

To establish the independent variability of parts requires a much closer study of possible correlations than has yet been made. The task is rendered particularly difficult by the varied combination and segregation of ancestral tendencies, which we have just considered. If we can account for the independence of certain characters on the ground of combining and sorting ancestral tendencies as wholes, one has to disprove the possibility of applying this explanation of the appearance of a partic-

ular variation before the latter can be regarded as giving evidence of a corresponding determinant. The burden of proof is on the shoulders of the upholders of the doctrine of determinants and it is a far heavier one than the champions of this doctrine commonly appreciate. Let us suppose that among the various sets of hereditary tendencies that find expression in the organization of an individual one should include the production of a particular variation in a single small part. The constitutional differences which may go along with this peculiarity and of which it may be regarded as one expression may be modified or kept from becoming manifest by other and rival sets of hereditary tendencies thereby rendering it almost impossible to detect the correlations that really exist, and giving the character the delusive appearance of independence. The question of the independent variability of parts is a crucial one for the particulate theories of inheritance, but it is one so beset with practical difficulties that a final answer may not soon be forthcoming.

In the preceding discussion the attempt has been made to show that the various categories of variations recognized by De Vries and others are not sharply separable either on morphological grounds or by their behavior when subjected to crossing experiments. The attempt was made also to show that neither the facts of variability nor those of Mendelian inheritance give any support to the doctrine of pangens, determinants, or other assumed bearers of unit characters, and that unit characters, as elements than can enter or depart from the complex of tendencies that make up an organism probably have no existence. It is evident that variations differ in their stability, but the explanation of this fact may lie in the physiological relations of the variation rather than in some hypothetical representative unit. Whether the variations of the discontinuous type have been influential, in any marked degree, in shaping the course of evolution is a question upon which we need much more evidence. Mutations, as we have seen, may be very small affairs.

About the only criterion by which they may be recognized is their stability, and even that gives some evidence of being a matter of degree. No limit has been discovered to the minuteness of the stable modifications that may occur, and it may happen that further study will reveal the comparatively frequent appearance of very slight variations of this kind. In fact, considerable progress has even now been made in this direction by the study of grains; and the number of more or less stable modifications that are likely to be discovered threatens to overwhelm systematists with the labor of naming and describing them. In many organisms not propagated by self-fertilization the detection of these small steps is no easy task and the attempt to describe them all would undoubtedly prove a futile effort. Among human beings, for instance, what are we to designate as elementary species? We meet with all grades of differences from well-marked family traits to those which separate the Caucasian from the negro. Are we to regard the Hapsburg lip which was transmitted with fidelity for many generations as the mark of an elementary species? It was apparently a new character and therefore presumably dependent upon a new pangen or determinant. The Celts, Teutons, Slavs, etc., differ by more or less constant characters which are constitutional and not confined to single parts, and the same may be said of the various subdivisions of these groups. The Aryan stock to which these groups belong is separated by still greater differences from the other subdivisions of the Caucasian race, and the latter in turn differs still more widely from the negroes and Mongolians. One has considerable difficulty in disposing of these groups either as varieties or elementary species. They can not from De Vries standpoint be considered the results of fluctuating variability on account of their constancy even under very varied external conditions. If the small divisions have arisen by slow changes, as everything indicates, there is no logical halting place short of admitting that the greater ones may have done

the same. In fact a survey of the racial differences of man in their varying degrees and kinds and their correlation with geographical distribution shows us pretty clearly that these differences have been slowly acquired by the summation of very small variations. These groups are not related as the so-called retrograde or digressive varieties are, but they are based on differences in general constitution affecting the shape of the skull, the characteristic complexion, the general temperament, and many other traits too numerous to specify. They may have arisen by minute, discrete, stable variations, but to call each step in advance an elementary species seems absurd, and to talk of the immutability of species still more so. We gain little by characterizing as elementary species the small steps of which there may be a dozen or more separating a German from a Frenchman.

Students of geographical distribution as a rule set little store by the theory of mutation. The relation of variation and species-forming to distribution as illustrated by the work of Gulick and Hyatt on the *Achatinellidæ*, the Sarasins on the snail fauna of Celebes, of Plate on the mollusca of the Bahamas, and of many students of the mammals, birds and fishes of North America indicate that the steps concerned in species-forming have been very modest ones. If sudden mutations of considerable magnitude have been a not uncommon source of varieties of domesticated animals and cultivated plants it does not follow that the selection of comparatively small variations has not been the predominant method of species-forming in a state of nature.

After fifty years from the publication of Darwin's "Origin of Species" we are still debating, and more lively than ever, the central problem of that epoch-making book; but it is not improbable the views of its sagacious author will prove more nearly correct than those of most of his modern critics. Much remains to be done before the problem is finally solved, and there are few fields

before the investigator that are more fruitful and alluring.³

³ *Mendelism and Unit Characters.*—Since this article on the Categories of Variation was sent in for publication several articles have appeared whose contents would have been referred to had they been published somewhat earlier. One of these is a short paper by W. J. Spillman in "The Nature of Unit Characters," in the April number of this journal, in which an interpretation of so-called unit characters is given which is, in many respects, similar to my own. Reference to Mr. Spillman's views would naturally be expected in an article appearing later than his in the same journal, so that it may be well to state that the proof of my paper was returned to the publishers in the first part of February, and that no modification of the paper has since been made. I am glad to find myself in agreement with Mr. Spillman at least to the extent that the facts of Mendelian inheritance do not compel us to adopt a particulate theory of heredity. That Mendelian inheritance can be explained by the sorting process which is supposed to take place in the reducing divisions of the germ cells I feel by no means assured, there are grave difficulties in the way of such an interpretation. But if this explanation prove to be the correct one it would be far from justifying the commonly accepted doctrine of unit characters with all its evolutionary implications.

Reference might also be made to some recent articles by De Vries, especially one on the crosses of *Oenothera nanella* (Ueber die Swillingsbastarde von *Oenothera nanella*. Ber. Bot. Ges. 26, p. 667, '08), inasmuch as the experiments reported tend to strengthen further the contention of the present writer that no sharp line can be drawn from the results of crossing experiments between elementary species and so-called retrograde varieties.

THE GENERAL ENTOMOLOGICAL ECOLOGY OF THE INDIAN CORN PLANT

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ECOLOGY being the science of the interactions between an organism, or a group of organisms, and its environment, and between organisms in general and their environment in general, this complex of relations may, of course, be divided in various ways. The division here used implies a centripetal grouping of the facts of relationship around single kinds of organisms, and the group of facts to be discussed is that of which the corn plant is the center and the insects of its environment are the active factors.

A prolonged study, extending over many years, of the entomology of the corn plant, the economic results of which have been published in my seventh and twelfth reports as State Entomologist of Illinois (the Eighteenth and Twenty-third of the office series) has left in my possession a considerable body of information capable of treatment from the standpoint of pure ecology, and the beginnings of such a treatment are here assembled because of the rising interest in ecological investigation and the promise which it gives of interesting and important results, and because of a wish to illustrate, in some measure, the general scientific value of such materials, of which, it scarcely need be said, the economic entomologists of this country have accumulated a large amount.

INSECT INFESTATION OF THE CORN PLANT

We know of some two hundred and twenty-five species of insects in the United States which are evidently attracted to the corn plant because of some benefit or advantage which they are able to derive from it. The

principal groups of this series are ninety species of Coleoptera, fifty-six species of larvæ of Lepidoptera, forty-five species of Hemiptera and twenty-five species of Orthoptera. The other insect orders are represented by seven or eight species of Diptera and one or two of Hymenoptera. Every part of the plant is liable to infestation by these insects, but the leaves and the roots yield the principal supplies of insect food, either in the form of sap and protoplasm sucked from their substance by Hemiptera, or in that of tissues and cells devoured by the subterranean larvæ of Coleoptera, and by caterpillars, grasshoppers and beetles, feeding above ground.

LACK OF SPECIAL ADAPTATIONS

Notwithstanding the great number of these insects, and the variety and importance of the injuries which they frequently inflict upon the corn plant, there is little in its structure or its life history to suggest any special adaptation of the plant to its insect visitants—no lure to insects capable of service to it, or special apparatus of defense against those able to injure it. The fertilization of its seed is fully provided for without reference to the agency of insects. It has no armature of spines or bristly hairs to embarrass their movements over its surface or to defend against their attack its softer and more succulent foliage. It secretes no viscid fluids to entangle them, and forms no chemical poisons or distasteful compounds in its tissues to destroy or to repel them. The cuticle of its leaf is neither hardened nor thickened by special deposits; its anthers are neither protected nor concealed; and its delicate styles are as fully exposed as if they were the least essential of its organs. Minute sucking insects are able at all times to pierce its roots and its leaves with their flexible beaks, and with the single exception of its fruit there is no part of it which is not freely accessible at any time to any hungry enemy. Only the kernel, which is supposed to have been lightly covered in the wild corn plant by a single chaffy scale or glume, has

become, in the long course of development, securely inclosed beneath a thick coat of husks, impenetrable by nearly all insects; and we may perhaps reasonably infer that, among the possible injuries against which this conspicuous protective structure defends the soft young kernel, those of insects are to be taken into account.

There are, of course, many insect species, even among those which habitually frequent the plant, which are unable to appropriate certain parts of its substance to their use, but this is because of the absence of adaptation on their part and not because of any special defensive adaptation on the side of the plant. Thus we may say that, with the exception of the ear, the whole plant lies open and free to insect depredation, and that it is able to maintain itself in the midst of its entomological dependents only by virtue of its unusual power of vigorous, rapid and superabundant growth. Like every other plant which is normally subject to a regular drain upon its substance from insect injury, it must grow a surplus necessary for no other purpose than to appease its enemies; and this, in a favorable season, the corn plant does with an energetic profusion unexampled among our cultivated plants. Insects, indeed, grow rapidly as a rule, and most of them soon reach their full size. Many species multiply with great rapidity, but even these the corn plant will outgrow, if given a fair chance, provided they are limited to corn itself for food.

Turning to the other side of the relationship, we may say that the corn insects exhibit no structural adaptations to their life on the corn plant—no structures, that is to say, which fit them any better to live and feed on corn than on any one of many other kinds of vegetation. This was, of course, to be expected of the great list of insects which find in corn only one element of a various food, and that not necessarily the most important; but it seems equally true of those which, like the corn root-worm or the corn root-aphis, live on it by strong preference, if not by absolute necessity.

Aphis maidiradicis, the so-called corn root-aphis, is not especially different in adaptive characters from the other root-lice generally, and it lives, indeed, in early spring, on plants extremely unlike corn. Finding its first food on smartweed (*Polygonum*), and on the field grasses (*Setaria*, *Panicum*, etc.), it is scarcely more than a piece of good fortune for it and for its attendant ants if the ground in which it hatches is sometimes planted to corn, in which it finds a more sustained and generous food-supply than in the comparatively small, dry and slow-growing plants to which it would otherwise be restricted.

The larva of *Diabrotica longicornis*, usually known as the corn root-worm, is, of course, well constructed to burrow young corn roots, but it differs from related *Diabrotica* larvæ in no way that I know of to suggest a special adaptation to this operation, except in the mere matter of size. If it were larger it would probably eat the roots entire, as does the closely related and very similar larva of *D. 12-punctata*. Indeed, there is some reason to believe that *D. longicornis* may breed in large swamp grasses, since the beetle has been found abundant in New Brunswick in situations where it is difficult to suppose that it originated in fields of corn, and where such grasses are extremely common. Even the special corn insects seem, in short, structurally adapted to much more general conditions than those supplied by the corn plant alone, and if they are restricted largely or wholly to this plant for food, this seems due to other conditions than those supplied by special structural adaptations.

In short, in the entomological ecology of the corn plant we see nothing whatever of that nice fitting of one thing to another, specialization answering to specialization, either on the insect side or on that of the plant, which we sometimes find illustrated in the relations of plants and insects. The system of relations existing in the corn field seems simple, general and primitive, on the whole, like that which doubtless originally obtained between plants in general and insects in general in the early stages of their association.

Such adaptations to corn as we get glimpses of are almost without exception adaptations to considerable groups of food plants, in which corn is included—some of these groups select and definite, like the families of the grasses and the sedges, to which the chinch-bug is strictly limited, and others large and vague, like the almost unlimited food resources of the larvæ of *Lachnosterna* and *Cyclocephala* under ground. These are evidently adaptations established without any reference to corn as a food plant, most of them very likely long before it became an inhabitant of our region, and applying to corn simply because of its resemblance, as food for insects, to certain groups of plants already native here.

ENTOMOLOGICAL ECOLOGY OF CORN AND THE STRAWBERRY

Corn being, in fact, an exotic or intrusive plant which seems to have brought none—or at most but one¹—of its native insects with it into its new environment, it will be profitable to compare the entomological ecology of this introduced but long-established and widely cultivated plant with that of some native species which is also generally and, in some districts, extensively grown.

We may take, for this purpose, the strawberry plant, whose insect visitants and injuries I studied carefully several years ago. About fifty insects species are now listed as injurious to the strawberry, and about twenty of these also infest corn. Two fifths of the known strawberry insects are thus so little specialized to that food that they feed on other plants as widely removed from the strawberry as is Indian corn. On the other hand, six species, all native, are found, so far as known, only, or almost wholly, on the strawberry, at least in that stage in which they are most injurious to that plant. These are the strawberry slug (*Emphytus maculatus*); the strawberry leaf-roller (*Phoxopteris comptana*)—occasionally abundant on blackberry and raspberry, to which it spreads from infested strawberry plants adjacent; two

¹ *Diabrotica longicornis* Say.

of the strawberry root-worms—the larvæ of *Typophorus aterrimus* and of *Scelodonta nebulosus*; the strawberry crown-borer (*Tyloderma fragariæ*); and the strawberry aphid (*Aphis forbesi*).

Not even one of this considerable list exhibits, so far as I can see, any special structural adaptation to life on the strawberry plant. The two root-worms mentioned, for example, are no better fitted to feed on strawberry roots than is a third strawberry root-worm—the larva of *Colaspis brunnea*, which lives on the roots of corn and timothy also. *Emphytus maculatus* might feed, for all the structural peculiarities which one can see, on the leaves of roses as well as does the common slug or false-worm of those shrubs—and so of the others of the list. Even the strawberry crown-borer, which lives in all stages solely on that plant, might, so far as structure and life history are concerned, feed and develop in any other thick-rooted perennial. The difference seems to be one of habit or preference solely, and not of structural adaptation.

Our impressions of the extent, nicety and frequency with which insects and plants are mutually adapted are indeed commonly much exaggerated, owing to the fact that our attention is especially drawn to notable cases of curious, precise or particularly advantageous adjustments between organisms, while no general study is made of the entire system of relations obtaining between all the members of an associate group, varying widely, as these do, in respect to the intimacy, importance and exclusiveness of the association. For this same reason, in part, we ordinarily have no accurate idea of the relative frequency and primacy of structural, or static, adaptations—particularly obvious, especially interesting, and seemingly ingenious, as they often are—and of those more obscure adaptations of preference, behavior, habit and the like, which, taken together, we may call dynamic.

CLASSIFICATION OF ADAPTATIONS TO FOOD

A plant-insect group—a group, that is, composed of a plant and its insect visitants—is not, in fact, usually marked, either as a whole or in any of its several parts, by the presence of adaptive structures special to that group. The structural adaptations of insects are, as a rule, much too broadly shaped to fit them closely to any one plant, and where such a fitting is found, it is clearly due to some other than the structural factor. Such facts bring us to a consideration of the whole subject of the variations and classification of the adaptations of insects to their food resources.

These adaptations may be classed as structural, physiological, psychological, synethic,² local, biographical and numerical. All structural adaptations are, of course, physiological, in a sense, but I use the word physiological, as a matter of convenience, for functional adaptations not based on obvious structural peculiarities, as where an insect equally capable of feeding on the sap of two plants, and readily availing itself of either, nevertheless thrives and multiplies better on one than on the other, the adaptation being evidently digestive or assimilative rather than obviously structural. The San José scale, for example, feeds readily on a great variety of trees and shrubs, on some of which it thrives poorly and spreads but little, while on others it multiplies enormously and spreads with great rapidity. The word psychological may be applied to cases of apparent choice or evident inclination, as between the various available food plants of the environment. Those fixed peculiarities of habit or behavior which adapt an insect to one food plant or class of food plants rather than to another we may call synethic adaptations, in the absence of any existing word applicable in this sense; local adaptations are those in which the usual haunts and places of resort of an insect species, however determined, bring it into common contact with an available food plant, the frequency of this

² Adaptations of habit.

contact being quite independent of the degree of the fitness of such plant for its food; biographical adaptations are those based on a correspondence between the life history of the insect and its organic food supply, such that the latter shall always be accessible in sufficient quantity to meet the varying needs of the dependent insect at the various stages of its growth; and numerical adaptations are the consequence of such an adjustment of the rate of insect multiplication to the plants or animals of its food that only the unessential surplus of this food shall be appropriated, leaving its essential maximum product undiminished.

These several classes of adaptations limit each other variously, the most desirable food of an insect being that which is found within the area common to all of them. That is, the most important food plants of a vegetarian species will be those which are well within its structural capacities of discovery, access and appropriation; within its physiological powers of easy digestion and profitable assimilation; and within its habitual range and location; and which are consistent with its usual preferences and habits of action, and are well adapted to furnish continuously amounts of food answering to its varying necessities during the different stages of its life.

ADVANTAGES OF BIOGRAPHICAL ADAPTATION

It is obviously to the advantage of any insect species that it shall have its largest possible food supply coincident with its own largest demand for food—that is, at the climax of its period of growth. In a species restricted to one annual food plant the most favorable relation will usually be that in which the life history of the plant and that of the insect coincide, the egg-laying period of the one corresponding to the seeding period of the other, the hatching of the insect being virtually simultaneous with the germinating period of the plant, and the period of most rapid growth being coincident in both. This kind of adaptation is well illustrated by the life histories of

Diabrotica longicornis and the corn plant. This beetle lays its eggs in fall when the ear is maturing, and the larvæ hatch in spring when the corn plant is young and growing slowly, and they feed on the roots during the entire growing season of the plant. It is evident that such a well-adjusted insect will have an advantage, other things being equal, over a poorly adjusted competitor for food from the same plant, since it will be able, as a rule, to leave a more vigorous and abundant progeny; and similarly, any part of a species which, by aberration of life history, may come to be poorly adjusted to its food plant, will suffer as a consequence in comparison with the normal members of the species, with the result that these biographical characters of the insect will tend to become permanent and characteristic in the same sense in which its structural characters are.

It should be noticed, also, that such an adjustment is an advantage to the host plant as well as to the dependent insect, since it distributes the depredations of the latter in a way to make them relatively slight when but little injury can be borne, and concentrates them, on the other hand, where the largest injury can be supported with the least serious consequences. Such a well-adjusted insect will get the maximum amount of food with the minimum injury to the plant, and such a plant-insect pair will have a competitive advantage over a poorly adjusted pair in which a greater injury is done to the plant than is necessary to the maintenance of the insect.

The same reasoning applies, and the same rule holds good, for species with a more heterogeneous food, except that in respect to them we must substitute for the single plant the entire group of plants to which the insect resorts for food. At this point, however, the facts become too complicated for successful analysis, especially in view of the difference of abundance from year to year of the plants of a considerable list, and the effects, on the food supply, of variable competitions among the various species resorting to it. It may be said, in general terms, how-

ever, that when the life history of a food plant, or the common history of a group of such plants, exhibits sufficiently constant characters to serve as an adaptive matrix, an adaptation to it of the life history of those insects strictly or mainly dependent on it for food is more or less likely to follow.

MUTUAL BIOGRAPHICAL ADJUSTMENTS OF COMPETITORS

An example of the competitive relations into which corn insects of widely different character, origin, habit and life history may be brought by their dependence on the same food plant may be found in *Diabrotica longicornis* and *Aphis maidiradicis*. Both pass the winter as eggs in the earth of the corn field, the aphid hatching sooner than the root-worm, and developing two or more of its short-lived generations before the *Diabrotica* larva is out of the egg, gaining thus the advantage of an earlier attack in greater numbers. It is also able to take much more rapid possession of a field of corn because of its command of the services of ants in finding its way to the roots of the plants which the tiny and feeble *Diabrotica* larva must search out for itself.

Later the root-aphid gives origin to young, many of which acquire wings and may thus disperse as their local attack upon the plant becomes unduly heavy, while the root-worm must take its chances for the year in the field where the eggs were left the previous fall. The aphid feeds at first on the sap of young weeds common in spring in all cultivated fields, and may thus save itself even though the ground is planted to wheat or oats, an event which causes the death by starvation of every root-worm hatching from the egg.

In respect to rate of multiplication, the root-aphid has, of course, a truly enormous advantage as compared with the corn root-worm, and yet, notwithstanding all these facts favorable to the aphid, its injuries to corn in Illinois are seemingly no greater than those done by the corn root-worm. This is due partly to the fact that, through

the winged members of the early generations, the percentage of which increases as conditions become locally less favorable, the aphid largely leaves the field in which it originally started, and early breaks the force of its attack by a general distribution of it. The depredations of the root-worm, on the other hand, increase with the growth of the insect until about September first, and increase also, at a rapid rate, from year to year in a field kept continuously in corn. It follows, as a consequence, that the principal damage by *Aphis maidiradicis* is done to the corn while it is young, and that by *Diabrotica* to the well-grown plant.

This serial order of injuries to the corn plant, due to the relation of the life histories and rates of multiplication of these two competing insects, is an advantage to both of them, and, indeed, to all three, corn included, since the plant would be more seriously injured or more certainly destroyed if both its insect enemies attacked it together than it is where their attacks are made successively. Competitors for food from a living plant find it to their advantage, and to that of the plant they feed upon, to avoid a simultaneous competition; and such a plant-insect group would, of course, prevail, other things being equal, over a competing group not so adjusted. Natural selection tends, no doubt, to establish these mutually advantageous relations between a plant and its constant insect visitants. With respect to these two corn insects, however, it must be admitted that no proof is apparent that such adaptation of life histories and habits as we here see is due to anything more than an accidental collocation of species whose significant peculiarities were already established when they came together.

A similar but more striking example of a serial succession of injuries to the same plant is to be found among the strawberry insects, as I showed several years ago.³ Three coleopterous larvæ belonging to the same family

³"On the Life Histories and Immature Stages of Three Eumolpini," *Psyche*, Vol. 4, Nos. 117-118, January-February, 1884; and No. 121, May, 1884.

(Chrysomelidæ) but to different genera (*Colaspis*, *Graphops* and *Typophorus*), and to species native in the United States, are all so closely adapted to underground life and to the root-feeding habit that they are distinguishable from one another only by rather slight and inconspicuous characters. They are often associated in large numbers in the same fields, living wholly on the roots of strawberry plants, which they affect in an identical manner, so that from the appearance of the injury itself one could not possibly tell which of the three species was present in the field. One of these root-worms, the *Colaspis* larva, feeds also on the roots of other plants, especially on those of timothy and corn, but the two other larvæ have been found only among strawberry roots. They seem thus to be strict competitors for food from the same part of the same plant, and as their locomotive capacity is poor, they are unable to avoid one another's company by migration under ground.

The strawberry plant, however, grows continuously throughout the season, and each of these three insects, having a short larval period, feeds on strawberry roots for only a part of this growing season. It is an interesting and striking fact that the life histories of the three competing insects are so related that the larvæ do not infest the plant at the same time, but follow one another in close succession, beginning early in May and ending late in the fall. The first of the species, the *Colaspis* larva, feeds from about May, to the end of June, the *Typophorus* larva follows in July and August, and the *Graphops* larva begins in August and continues until fall.

Consistently with this difference, the species concerned hibernate in different stages of development—*Colaspis* apparently as an egg, *Typophorus* undoubtedly as an adult, and *Graphops* as a larva in its subterranean cell, from which adults emerge the following June to lay their eggs in July. With such a distribution of their attack, each of these three species is able to maintain itself on the strawberry in numbers as large as would be possible for

all three taken together if they made their assault on the plant simultaneously. The advantage to both plant and insects of this adjustment of life histories—if one may call it such—is obvious at once.

That some actual adjustment of larval periods has here been made is rendered somewhat more probable by the fact that a closely related species of *Graphops* which infests the wild primrose (*Enothera biennis*) in southern Illinois, has a life history different from that of the species which breeds in the strawberry—hibernating as an adult, like *Typophorus*, and not as a larva, like the strawberry species of its own genus.

MALADJUSTMENT OF COMPETITIONS

The corn plant is in greater danger from insect ravage during the first month of its life than at any later time. This is because it offers then a comparatively scanty supply of food, so that a small number of insects may work great destruction; because the single small plant is much more easily killed than a larger one; and because a larger number of active rival insects infest corn when it is young than at any other time, some of them beginning with the recently planted or just sprouting seed. The young roots, the underground part of the stalk, the stalk above ground, and the leaves, both before and after they unfold, are all liable to infestation by several species at the same time. The seed is injured by the wireworms, the seed-maggot, the *Sciara* larva and the larva of *Systema blanda*; the roots, by the wireworms, the root-aphis, the corn root-worms, and the white-grubs; the stalk under ground, by the wireworms, the root-aphis, the southern corn root-worm, and the bill-bugs; the stalk above ground, by the bill-bugs, the cutworms, the web-worms, the stalk-borers, and the army-worm—sometimes by the chinch-bug also; and the leaves, by the bill-bugs, the web-worms, the cutworms, the army-worm and the first generation of the ear-worm.

This concentration of injury upon the corn when it is

young is a case of maladaptation, since the plant has least to offer when it is most heavily drawn upon. It will be noticed, however, that this early spring attack is mainly delivered by insects which come into corn from some other vegetation, chiefly from grass, and whose occurrence in the corn field is scarcely more than accidental. The motive to an adjustment of habits and life histories to the capacities of the plant is therefore virtually wanting, and seems at any rate impossible, owing to the variability and inconstancy of the several factors involved.

CONCLUSION

From the foregoing it will be seen that the corn plant is not only an exotic in its origin, but that, aside from its relation to man, it still remains an unnaturalized foreigner, not sufficiently adapted to our conditions to survive without the constant supervision of a guardian and the services of a nurse. The corn field contains an artificial "association" persistently maintained by human agency in the midst of a hostile environment, to which it would promptly succumb if left to itself, and as such it would seem to offer to the ecologist all the advantages of a vast and long-continued experiment, by a study of whose results he may learn something of the manner in which ecological relations may be affected when a plant takes advantage of a single favoring condition to push its way into a territory foreign to its former habits.

This corn plant, at least, which has certainly lived in our territory under the care of man for several centuries, and perhaps for some millenniums, has even yet no specialized friends active in its service, and no structurally adapted enemies enlisted against it, such specializations of injurious relationship as one detects being clearly due to other than structural differentiations. During all this long period, it has been widely and steadily forced into a strange ecological system which has nevertheless scarcely yielded to it at any point. It has produced, it is true, by its enormous multiplication and

extension, a profound effect on the numbers and distribution of some insect species, reducing the area of multiplication for several, which, like the cutworms and the army-worm, formerly bred in the turf of our native prairies, but can not breed in fields of corn; and immensely extending the range and increasing the number of others which have found in this plant a better and far more abundant food supply than that originally available to them. Insect species which, like *Diabrotica longicornis* and *Aphis maidiradicis*, were almost unknown fifty years ago within our territory, have now, through their increase in cornfields, arisen to the rank of dominant species.

But the few discernible insect adaptations to the offerings of the corn plant are physiological, psychological, synethic and biographical, and apparently not structural at all. Slight and seemingly incipient as they are, we have no sufficient reason to conclude that they are recent results of the association of the corn plant with the insect; both parties of the association may have been substantially what they now are when they first found each other, and such mutual fitness as they exhibit may be merely like that of angular stones shaken together in a box until like surfaces seem to cohere, simply because in this position the fragments can not readily be shaken apart.

We may also derive, from this discussion, support for the idea that adaptations of insects to their environment are largely, and often primarily, psychological—that they are often, in the first instance, specializations of preference or choice, or, as we may perhaps more safely say, of tropic reaction. Species which would otherwise compete with each other, with disadvantageous consequences to each, escape these disadvantages by acquiring, one or both, different habits of reaction, under the influence of which they separate, one going for its principal food to the corn plant, for example, and the other continuing on the strawberry, although structurally each remains equally fit to feed on either. Physiological, or even struc-

tural, adaptation may follow the psychological, but as secondary to it. This is only saying in other words that the central nervous system, on which special functioning peculiarities of habit depend, is subject, like any other, to adaptive variations, and that these variations may either follow and reinforce those of some other organ or organs tending to the same end, or that they may arise independently of any other; and this is merely extending to insects a generalization very obvious with respect to man—finding warrant for the extension, as we do, in the facts disclosed by an examination of the general economy of insect life.

NOTES AND LITERATURE

BIOMETRICS

Some Recent Studies on Growth.—The problems presented by the phenomena of growth change are not only peculiarly adapted to quantitative treatment, but perhaps more obviously and clearly demand the application of quantitative methods for their solution than does any other single large class of biological problems. In the study of variation and heredity it is an open question as to what relative importance is to be assigned to quantitative as compared with qualitative differences between organisms. But however much interest or significance qualitative changes occurring in connection with the growth process may have, it yet remains an indisputable fact that the fundamental and essential feature of the process is a quantitative change. While this has, of course, always been recognized by students of the subject, there still is to be seen evidence of the influence of the modern biometric standpoint in recent studies in this field. This is chiefly apparent in the increasing attention paid to precision and refinement in the mathematical methods used in the analysis of the distinctively quantitative phases of the problems of growth.

The most recent contribution in the series of memoirs by Professor H. H. Donaldson¹ and his students dealing with various phases of the problem of growth in the white rat is in some respects to be regarded as the most fundamental which has yet appeared. This paper gives in detail the basic data regarding the growth of the body as a whole and of the central nervous system in the white rat which have been collected in the course of a very extensive and thorough investigation. These data are given in a "general table" occupying thirteen pages and comprise records for 458 male and 215 female normal white rats. For each of these animals (with the few omissions of single measurements in scattered individuals unavoidable in so large a piece of work) there are recorded the following data: Series

¹ Donaldson, H. H. A Comparison of the Albino Rat with Man in Respect to the Growth of the Brain and of the Spinal Cord. *Journ. of Comp. Neurol. and Psychol.*, Vol. XVIII, pp. 345-392, Plates II and III, 1908.

number, sex, age in days, body weight, brain weight, and spinal cord weight, each in grams. That the utmost care was taken to ensure the accuracy of these weight records really does not need saying in an American biological journal. The body weights are recorded to a tenth of a gram, and the brain and cord weights to a ten-thousandth of a gram. These unique data, involving thirteen years in the collecting, constitute a scientific achievement of much significance, not alone because of the intrinsic importance of the records for the study of growth problems, but also because they are a monumental example of biological data collected with physico-chemical exactness. The paper will stand as a classic in the literature on growth.

The first portion of the paper deals with the growth of the rat's brain. The brain-weight data are plotted to a base line of body weight instead of to a base line of age and when so arranged are graduated with a curve of the general type.

$$y = A + C \log (x + \beta)$$

where y denotes brain weight, x body weight and A , C and β are constants.

The actual theoretical curve for the brain weight of the white rat is as follows:

$$y = .569 \log (x - 8.7) + .554.$$

This curve gives a very excellent graduation of the observational data. In fact, a closer agreement between theory and observation could not reasonably be expected. It is of some interest to note that this curve which describes the growth of the rat's brain in weight is of the same general type which has been found by Pearson and by the present writer to describe growth changes in various organisms.² It is all the time becoming more evident that this type of curve is a very useful one for growth work. Experience is showing that it undoubtedly has a wide range of applicability in describing the quantitative changes occurring in growth and various sorts of regulatory phenomena. While this fact is empirically obvious, no ulterior biological significance is to be attached to it. The biological significance of this fact appears to the present writer to be of the same *kind* as would attach to the discovery that some particular stain was useful for differentiating a wide range of cell

² Cf., for example, the data regarding growth in the plant *Ceratophyllum* presented in Carnegie Institution Publication No. 58.

structures, not before known to have anything in common. Such a result *might* mean that these structures all had a common cause or mode of origin, but to draw such a conclusion in the absence of confirmatory evidence of another kind than that afforded by the stain would be an exceedingly hazardous proceeding.

Donaldson points out that while the logarithmic curve describes very well the growth of the brain for the whole period from birth to maturity, the simpler relation proposed by Dubois, according to which the brain weight increases as some simple proportion (here the seventh root) of the body weight, fails to do this, since it holds only for the later growth period of the rat's brain. It fails entirely to graduate the data during the period of rapid growth.

The second portion of the paper deals with the growth of the spinal cord. This again is found to follow a logarithmic curve of the same general type as that which graduates the brain growth data though, of course, with different values of the several constants. Succeeding portions of the paper deal with the growth of the entire central nervous system and with the comparison of the growth of the brain in the rat and in man. Limitations of space forbid a detailed discussion here of the numerous significant results set forth in the paper. Certain points of particular interest from the biometric standpoint may, however, be touched upon briefly. First with regard to the correlation data, Donaldson finds that the weight of the brain in the white rat is very closely correlated with body weight, the coefficient of correlation between these two variables being $.76 \pm .01$. This appears to indicate a very much closer relationship in this organism than in man, though of course it must always be remembered that the body weight data for man which have been available for the study of this correlation are autopsy records and therefore not too trustworthy. The correlation found between brain weight and age is also very much higher than the corresponding correlation in the case of man, the coefficient here being $.52 \pm .03$. The spinal cord weight is found to be even more closely correlated with body weight than is brain weight; the coefficient being $.86 \pm .01$. Here there are no human data available for comparison. The data presented also indicate a very high degree of correlation between the weight of the brain and the weight of the spinal cord. The coefficient of

correlation here is $.88 \pm .01$. All of these correlation coefficients are positive.

The high values of these correlation coefficients for the rat as compared with man suggest an interesting question: Are we to conclude on the basis of these results (and similar ones obtained by Kellicott from his study of the toad) that there is a general tendency for the various parts of the body to be more closely correlated in lower organisms than in man? In the writer's opinion such a conclusion is at present very doubtful for two reasons. In the first place the human data on which correlation studies have been made are meager and, from their method of collection, not altogether trustworthy. In the second place the coefficients of correlation published by Donaldson (the same considerations hold with reference to Kellicott's toad data, though not to so great a degree relatively) probably have spuriously high values. This arises from the fact that they are deduced from material which is very heterogeneous in respect to age. The biometric constants for all characters which change with age by growth will have their values affected in such material. It is a well-known fact, of which the mathematical proof was first given by Pearson, that heterogeneity of material operates to increase apparent correlation. To such an extent may this occur that several sets of data, each of which taken alone shows no correlation whatever between two characters, may when combined exhibit a high degree of correlation between these characters. Such correlation obviously has little, if any, biological significance. In the work here under discussion no account is taken of the possible effect in increasing apparent correlation of the age (= growth) heterogeneity of the material. It seems desirable if brain-weight (or other) correlations are to have full significance for comparative purposes, that they be based either on adult material in which all growth changes have reached a minimum, or at least on material which is homogeneous in respect to some definitely marked period of the life cycle.

A further point of less practical significance which is apparently overlooked by Donaldson in his discussion of correlation results is that in at least all of his cases in which the regression lines are plotted in the paper the correlation is markedly skew. In such cases, of course, the correlation coefficient can not be taken as the true measure of the actual correlation. Instead, resort must be had to the correlation ratio (η).

The facts regarding the sex relations in the weight of the central nervous system and its growth in the rat are very interesting. Just as in man the brain of the male rat is absolutely somewhat heavier than is that of the female rat of the same body weight. The difference, however, is very small. It is believed by Donaldson that this small difference which remains in favor of the male in respect to brain weight is probably open to further reduction as other variables are taken into account. In general the quantitative relations of the growth of the central nervous system are found to be similar in man and the white rat.

A paper with very much the same general standpoint as the one just discussed has recently been published by Kellicott.³ The immediate problem with which this paper has to do is stated in the following words (p. 319):

We are led to inquire whether the normal growth of an animal may not be actually a complex of growth cycles of component parts. It is quite possible to examine this question from the morphological as well as from the physiological side and the present paper represents an attempt to discover whether the brain and viscera of the dogfish grow similarly or in diverse ways as somewhat independent units of growth.

The investigation is based on data obtained from a series of 315 dogfish (176 females, 139 males) including specimens from birth up to those of large size and presumably considerable age (maximum weight observed 8,434 grams). On these fish the weights of the following organs were determined: brain, heart, rectal gland, pancreas, spleen, liver and gonad. In addition the total body weight was determined in each case. The weighings were made in all cases except body weight to hundredths of a gram.

Since it was impossible to determine the exact age of the specimens, the whole of the material is dealt with from the standpoint of total body weight as a base. The author justifies this procedure on two grounds, one necessity, and the other that such factors as "food and temperature are known to be of more importance than age in determining the size of fish."

The specimens studied do not represent a random sample of a fish population, but were especially selected to get a represen-

³ Kellicott, W. E. The Growth of the Brain and the Viscera in the Smooth Dogfish (*Mustelus canis* Mitchell). *American Journal of Anatomy*, Vol. VIII, pp. 319-353, plates 1-7, 1908.

tative size series. The data so obtained were plotted, each individual being entered separately. Smooth curves were then derived from these and the bulk of the paper is occupied with a discussion of the facts brought out by these smoothed curves. The only statement as to how the observational data were smoothed is the following (pp. 322-323):

The curves were derived from these records by calculating a series of average weights of each organ in successive groups of individuals and a line formed by connecting these averages was then smoothed to a curve so as to reduce to a minimum the plus and minus deviations of the averages. The groups from which the averages were derived varied in extent from 100 to 1,000 grams in different regions of the entire group, according to the rate at which the character of the curve was changing.

From this the inference would appear to be that the smoothing was done by a free-hand graphical process. If this inference is correct the logical justification of the procedure in the present case is difficult to see. If the curves have enough intrinsic significance to warrant smoothing at all (as these for the dogfish certainly do) it is hard to understand why the smoothing should not be done by an accurate method. Of course cases will arise in practical work where the points to be brought out by data are not of sufficient importance to warrant the labor involved in graduating them accurately. But in the present case the whole discussion centers about the forms and relationships of the smoothed curves.

The point involved here is not a trivial or insignificant one. Any one who has had experience in fitting parabolas and similar curves to observational data knows what unexpected effects on the general contour of a curve a few outlying points may have, when the rigidly "fair" method of least squares is used in the smoothing. The difficulty may be put in this way: in curves of the sort dealt with by Kellicott the observations are very scattering over a considerable part of the total range of the curve. In many instances only two or three observations will be averaged to get a point on the smooth curve. But surely it can not be maintained that the average given by two individuals will uniformly be the same as would appear if 25 individuals were to be used. The two individuals may happen to be the mediocre ones which will give nearly the true average; but on the other hand they are not unlikely (as the right-hand ends of

all of Kellicott's curves except that for brain weight clearly show) to be widely divergent from mediocrity. But the "free-hand" method of smoothing assumes, actually if not intentionally, that the average based on two individuals is just as "right" (*i. e.*, expressive of the true relationship which it is the purpose of the investigation to discover) as is that based on 25. This obvious error any adequate method of curve fitting will avoid.

The bearing of these remarks further appears clearly in the case of some of the relative curves, wherein the percentage which the particular organ weight is of the total body weight is plotted. As was to be expected from what is known of growth in man the general trend of these percentage curves is downward. While this is the general trend, several of the curves (*e. g.*, the heart curve, plate 2) show at the very beginning a slight rise to a maximum and then the downward curve. It is plain from the discussion that Kellicott considers the rise at the beginning of these percentage curves to be a real and significant phenomenon of growth. It is very doubtful, however, whether the data warrant such a conclusion. Before accepting it one would like to see the measurements of a much larger number of very young (*i. e.*, just hatched) individuals added to the curves, and then have a curve fitted by some adequate method to the observations.

The general result of this interesting and careful piece of work is to show that the regression line of organ weight on body weight in dogfish of different sizes is not of the same form for all organs. Some organs (*e. g.*, rectal gland, pancreas) show a nearly linear increase in weight as the body increases in size; others (*e. g.*, the brain) show the logarithmic like curve which one associates with growth curves. The author gives an interesting discussion of the significance of the fact that the muscular and skeletal tissues tend to "outgrow" their visceral accompaniments in forms of indeterminate growth like the dogfish. He regards the condition of determinate growth seen in higher vertebrates as "an adaptation on the part of the organism, such that muscles and supporting tissues cease their growth at such a point that brain and viscera remain competent to maintain a physiological balance."

In passing it may be noted that Kellicott's work, while itself strictly morphological, suggests on every page problems for experimental work on the physiology of the growth process. In

this connection a recent paper by Burnett⁴ is of interest. This paper, though not specifically concerned with growth problems as such, brings out in a very clear way the marked differential effect which may be produced on a single organ system (the skeleton) by differences in the food of the growing animal. Different foods, with all other conditions constant, led to an average difference in the breaking strength for five bones of the body of 356 pounds per 100 pounds body weight. The relative magnitude of this difference is indicated by the fact that the *maximum* observed average breaking strength was 681 pounds per 100 pounds of body weight. This difference is brought about not by an increase in the size of the bone as a whole, but by a thickening of its walls. Burnett's detailed results are well worth careful study from the standpoint of experimental morphology.

A new and suggestive view in regard to the ultimate physiology of the growth process has been put forth recently in two papers by Robertson.⁵ In brief this view is stated by the author in the following words (first paper, p. 612):

1. In any particular cycle of growth of an organism or of a particular tissue or organ of an organism the maximum increase in volume or in weight in a unit of time occurs when the total growth due to the cycle is half completed.

2. Any particular cycle of growth obeys the formula $\log x/(A - x) = K(t - t_1)$ where x is the amount (in weight or volume) of growth which has been attained at time t , A is the total amount of growth attained during the cycle, K is a constant and t_1 is the time at which growth is half completed.

3. The above relations are such as would be expected to hold good were growth the expression of an autocatalytic chemical reaction. As I have pointed out in the introduction, cell-division has been shown by Loeb to be the expression of an autocatalytic synthesis of nuclear material. The fact that the above relations hold good shows that, in all probability, cell-growth, or the synthesis of cytoplasm, is also an autocatalytic reaction.

These conclusions, if well founded, are certainly of very fundamental importance. It therefore seems desirable to ex-

⁴Burnett, E. A. The Effect of Food on the Breaking Strength of Bones. Bulletin 107, Nebr. Expt. Stat., pp. 11-39, 1908.

⁵Robertson, T. B. On the Normal Rate of Growth of an Individual and its Biochemical Significance. *Arch. f. Entwicklungsmech.*, Bd. 25, pp. 581-614, 1908. Further Remarks on the Normal Rate of Growth of an Individual and its Biochemical Significance. *Ibid.*, Bd. 26, pp. 108-118, 1908.

amine with some care the nature of the reasoning and the evidence on which the conclusions rest. The first point in this regard to be noted is the fundamental assumption made by the theory that the growth process is in its quantitative relations *determinate* either as a whole, or in its cyclical units. In the fundamental formula quoted A is the total amount of growth attained in the cycle. This means that unless there is assumed to be an indefinitely large number of cycles of growth, there comes a time for every organism to which the theory is to be applied, after which no more growth occurs. Regarding this fundamental assumption of Robertson's theory Kellicott, whose own researches particularly well fit him to speak with authority on the point, has the following to say (*loc. cit.*, p. 342):

Observations of many of the lower vertebrates in nature (Fulton, '01, '06) and in captivity, such as the giant salamander and some reptiles, show that these grow indeterminately; Agassiz's, '57, observations upon *Chrysemys* are typical. As a recent example of the failure to make this distinction we might mention the work of Robertson, '08, who has devised certain formulæ for the description of growth and has brought out the very suggestive fact that the growth curve of an organism or organ or tissue is similar to that given by an autocatalytic reaction. These formulæ hold good upon the assumption that the organism or organ has a definite period of growth at the end of which increase in size ceases. This is true for the higher vertebrates, but for all the indeterminately growing forms we can not determine any such "final weight" of the body or organ upon which to base a formula. We could not assume the maximum discovered size as the "final weight" because this is subject to such extreme variation; in the dogfish, including both sexes, we might find the "final weight" anywhere from 2,000 to 8,000 grams and even higher.

That this point has some force in limiting the field of application of Robertson's view can not be denied. It would still appear to be possible to apply the theory to lower vertebrates and invertebrates, however, on the assumption that growth in those cases consists of an indefinite number of cycles, to each one of which separately the "law" applies. It remains to be investigated as to whether the growth in such forms is, as a matter of fact, definitely cyclical in character.

The general line of reasoning adopted by Robertson in developing his theory of growth is as follows: The starting point is the idea advanced by Loeb "that the process of synthesis of nuclein, which is the most salient phenomenon immediately suc-

ceeding fertilization, partakes of the characteristics of an autocatalyzed chemical reaction, since the velocity of the synthesis increases, during the initial stages of cell-division, in proportion as nuclear material has already been synthesized." He then raises the question as to whether the formation of fresh cytoplasm during the growth of an organism may not also be an autocatalytic reaction. It is pointed out that:

The increase in weight or volume of an organism may not improbably be regarded as equivalent to an increase of cytoplasm, and if both of the processes concerned in growth, namely nuclear and cytoplasmic synthesis, are autocatalytic in character the increase in weight or volume of an individual with increase of time should display the quantitative relations which are characteristic of an autocatalytic chemical reaction. In the first place the temperature coefficient of growth should be that of a chemical reaction; in the second place the relation between body weight or body volume and the time which has elapsed since measurable growth began should be the same relation as that which subsists between the mass of material which has undergone a chemical change and the time in an autocatalytic reaction.

This work of Peter is cited to show that the temperature-coefficient of cell division and of growth is that of a chemical reaction. Robertson's own papers are solely concerned with the presentation of evidence to show that growth curves of organisms are of the same type as the curve of an autocatalytic reaction.

Various observations on the growth of certain animals, plants and man are cited from the literature. To each group of these data the theoretical curve of an autocatalytic reaction is fitted. Theoretical and observational curves are then compared, and it is maintained that the graduations obtained are good ones. The agreement between observation and theory which is held to be shown by these comparisons is the only new evidence presented by Robertson in support of the conclusions quoted above.

The data presented in the papers may first be considered with reference to the soundness of the contention on which the whole reasoning ultimately rests: namely, that the theoretical curve for an autocatalytic reaction actually does give a good fit for observed growth data. A careful, critical study of the data presented in the two papers indicates that in general the correspondence between theory and observation is very far from being sufficiently close to warrant the conclusion that such is the case. To bring this point out in a concrete fashion let us

examine some of the tables given. Table I of the first paper (pp. 581-591) deals with Donaldson's^a data on the growth of the male white rat in respect to body weight. In this table are given the observed body weights for rats of different ages and the calculated body weights according to the autocatalytic growth curve. In addition there is given a column showing the differences in grams between the observed and the calculated body weights. Now it is a first principle of scientific curve fitting (and on this point science and common sense are as usual in agreement) that a curve which gives a good graduation of observational data will fairly and equably distribute the errors. That is to say, a theoretical curve if it is to be regarded as fitting the data should strike through the observations in such way that there will be on the average as many and as great differences where theory is in excess of observation as there are where it is in defect of observation. If a great majority of the differences between theory and observation are in one direction there is clearly a bias and the theoretical curve can not fairly be said to be an adequate representation of the observations. Now, let us examine the actual facts for Robertson's Table I. In this table are included 63 separate observations or ordinates. In one case out of the 63 the theoretical and the observed ordinate exactly agree. Of the remaining 62 cases where theory and observation can be compared the calculated ordinate is greater than the observed in only 14. The observed ordinate is greater than the calculated in 48 cases out of the 62. Furthermore, the total deviation between observation and theory when theory is greater than observation is 19.6, whereas when observation is greater than theory the total deviation is 706.0! This certainly does not look like a fair distribution of the errors when in 77 per cent. of the ordinates the theoretical curve lies always on the same side of the observational line.

Let us turn to Table II. This table is exactly like Table I except that it deals with Donaldson's data for the growth of female white rats in body weight, whereas Table I deals with the males. In this table there are in all 50 ordinates. Of these one again shows an exact agreement between observation and theory. In 43 or 88 per cent. of the remaining 49 ordinates the calculated value is less than the observed. Only in 6 cases is the calculated value greater than the observed! Practically the

^a Boas Memorial Volume, New York, 1906.

whole of the theoretical curve in this case lies on the same side of the observed line. The sum total of the plus deviations equals only 1.15, whereas the sum total of the minus deviations equals 199.05!

Let us take still another example, this time from near the end of the first paper. In Table IX (p. 610) are presented Donaldson's⁷ data regarding the growth of the brain in the frog and the fitted curve. In this table are 21 ordinates available for the comparison of theoretical curve and observational data. The deviation between theory and observation is plus in 18 out of the 21 cases and minus in 3 cases only. Two ordinates (making with the 21 the total of 23 tabled) show exact agreement between theory and observation. In spite of this extraordinarily uneven and biased distribution of the errors this statement follows Table IX:

It is evident that the agreement between theory and observation is excellent, such divergences as exist being evidently irregular and accidental in their nature.

Surely a system of errors in which 86 per cent. are in excess and only 14 per cent. are in defect and in which the *mean* percentage deviation per ordinate for the plus deviation is 8 per cent. can not fairly be said to be "irregular and accidental" in its nature.

Other examples showing the same thing might be cited from the papers. The tables which have been chosen as illustrations of the point under discussion have been taken in preference to others for two reasons; one that they were long tables, involving a fairly large number of ordinates, the other that the observational data in these tables were obtained by most careful and painstaking measuring and are absolutely trustworthy. On such data, if anywhere, a theoretical curve may fairly be expected to give good results.

To summarize this part of the discussion it may be said that the discrepancies between observation and theory are so great in amount, so biased in character and so frequent in the data presented that these data, as they stand, can not reasonably be held to afford evidence of any particular value in favor of Robertson's ingenious, suggestive and potentially very valuable hypothesis. It is possible that better values for the constants of the theoretical curves might be found and in this way better

⁷ *Jour. Comp. Neurol.*, Vol. VIII, 1898.

agreement between theory and observation be obtained. Until this is tried it would appear to be impossible to form any just and significant estimation, on the basis of the only *kind* of evidence which Robertson presents, namely, the comparison of curves, as to the value of his theory as a general theory of growth. On many general grounds the theory is particularly suggestive. Can not evidence of another and more convincing kind than that adduced in the present papers be brought forward in its support?

The kind of evidence under discussion, when used for a purpose like the present one, can at best have but inferential significance; it can never be of demonstrative worth. It is based on a process of reasoning which assumes a fundamental or necessary relationship to exist between two sets of phenomena because the same curve describes the quantitative relations of both sets. A little consideration indicates that this method of reasoning certainly can not be of general application, even though we assume it to be correct in particular cases. The difficulty arises from the fact that the mathematical functions commonly used with adequate results in physical, chemical, biological and mathematical investigations are comparatively few in number. The literature of science shows nothing clearer than that the same type of curve frequently serves to describe with complete accuracy the quantitative relations of widely different natural phenomena. As a consequence any proposition to conclude that two sets of phenomena are causally or in any other way fundamentally related solely because they are described by the same type of curve is of very doubtful validity. A few examples will make clear the point here under discussion.

In a recent paper Armsby* shows that the rate of gain of protein per thousand pounds live weight in growing animals follows extremely closely the following curve: $g = 135/(a + 20)$, where g is gain in protein per day per 1,000 lbs. live weight and a is age in days. This curve, as his Fig. 1 clearly shows, fits the observational data at hand remarkably well. This equation is the equation of a rectangular hyperbola. But it is a well-known fact that the relation between degree of dissociation and degree of dilution in dilute solutions is given by a hyperbola. Now in so far there would appear to be exactly the same

* Armsby, H. P. Feeding for Meat Production. Bureau of Animal Industry, Bulletin 108, pp. 1-89, 1908.

kind of logical basis for the conclusion that since the same curve describes the rate of protein gain in growing animals as describes dissociation phenomena, therefore rate of protein gain is a dissociation phenomenon, as would exist for the conclusion that growth is an autocatalytic reaction provided there were good agreement between observed and theoretical curves in the latter case. A point of difference in the two cases is that Robertson presents several curves in support of his conclusion, whereas Armsby gives but a single hyperbola. But even this difference is in some degree offset by the fact that Armsby's curve involves growth data from four different animals collected by a number of observers. But the most ardent advocate of the plan of deducing fundamental relationships from similarity of curve type would not maintain that the rate of protein gain in growing animals is in any causal or fundamental way directly related to the phenomenon of dissociation in dilute solutions.

Let us take still another case. One of the fundamental gas laws is that the "pressure of any given mass of gas varies directly as the absolute temperature if the volume of the gas remains constant." The mathematical expression of this relation is the equation of a straight line. Now Galton, Pearson and their co-workers have shown, with a wealth of data drawn from man and other organisms, that the regression of offspring on parent in parental inheritance is a linear function. If the mean conditions of a characteristic of the offspring of each group of parents be plotted these plotted points will fall on a straight line, within the errors of random sampling. This result rests on a great mass of exact measurements. But of course no one would attempt seriously to maintain that parental inheritance and regression are phenomena of gas pressure.

The point which the writer would make is this: If there is good evidence *on other than quantitative grounds* that two sets of phenomena are qualitatively alike it is pertinent and significant to present as additional and confirmatory evidence data tending to show that these sets of phenomena are similar in their quantitative relations. But similarity of quantitative relations between phenomena can not safely be taken as proof (or, in the absence of qualitative data sufficient alone practically to establish the point, even as particularly weighty evidence) of qualitative identity, because of the observed general lack of uniqueness in the quantitative relations of natural phenomena.

In a word the final *proof* of qualitative identity of phenomena must always in last analysis be qualitative in its nature; quantitative evidence in such cases can at best have but an inferential confirmatory bearing on the qualitative point at issue.⁹

RAYMOND PEARL.

EXPERIMENTAL ZOOLOGY

Are the Drone Eggs of the Honey-Bee Fertilized? Cuénot¹ has put to the test once more Dzierzon's famous theory in regard to the nature of the drones of the hive bee. Dzierzon, as is well known, furnished strong evidence in favor of the view that the egg that produces a drone is not fertilized. An obvious test of this view is found in crossing a virgin queen of one race by a male of another race. All of her worker offspring should be hybrids but her drone offspring should be purely maternal in character. It is said that the failure of one such experiment to give the expected results caused Dzierzon to abandon temporarily his theory. Other workers too have from time to time found that the drones in such cases sometimes show hybrid characters and this argument has been repeatedly urged against Dzierzon's theory despite the large amount of evidence of a different kind to the contrary.

Cuénot crossed a virgin female of the black or Italian bee of pure race with a "yellow bee" also of pure race. All the workers produced showed the yellow bands of the yellow parent; some 300 drones were black like the mother, two only showed a large yellow band at the top of the abdomen (recalling the more numerous yellow bands of the yellow bee), and about a dozen other males also showed some yellow bands on the abdomen. "Do those yellow bands indicate hybridization?" Such bands were never found in the males of neighboring hives. The experiment is inconclusive, Cuénot says, but it shows the necessity of examining not only the purity of the pure races but also the extent of their variation. The possibility that these few hybrid males may have arisen from eggs laid by the hybrid workers is not considered by Cuénot but until this possibility is also excluded the results can not be maintained to show the hybrid nature of the drones except in the latter sense. If the males

⁹ Cf. the discussion regarding the simple logarithmic growth curve on p. 304, *supra*.

¹ Cuénot, L. *Comp. Rend. Soc. Biol.*, LXVI, 1909.

have arisen as here suggested from the eggs laid by the hybrid workers the fewness of such individuals in comparison with the large number of pure males is explained. On the other hand the apparently well established view that drones come from unfertilized eggs does not exclude the possibility that fertilized eggs might also under certain exceptional conditions produce males.

T. H. MORGAN.

THE UPHOLDING OF DARWIN

Poulton and Plate on Evolution.—The boundary lines of political geography are supposed to have no influence in determining scientific beliefs. In science one is cosmopolite. But hedged in by a nation's boundaries is a people of one blood, men of a common genealogy, and hence of some identity of hereditary endowment. It may not be so easy, therefore, for an Englishman to be French in scientific tenets as he may imagine. The coincidence that the majority of conspicuous English biologists, such men as Wallace, Galton, Lankester, Archdall Reid, Edward Poulton and others, hold so strongly to the natural selection dogma, and, except for the German founder of the school, are the most outspoken upholders of neo-Darwinism, may be indeed more than a coincidence. It may be unconscious scientific patriotism. And so in France, there is no question of the strong leaning of present-day French biology toward Lamarckism. How much more pitiful, in the light of this fact, let us add, seem the neglect and contempt of the great French evolutionist in his lifetime by his Gallic colleagues! But he has now his reward. Scientific patriotism is bringing his name and his teaching to be the glory of French biology.

I would not press my theory too hard. As Weismann is the founder of neo-Darwinism the Germans ought to be neo-Darwinists, but they mostly are not; and as Haeckel is a monist, they ought mostly to be anti-dualists, but again they mostly are not. Also, as America is more Anglo-Saxon than Latin, we ought to be more Darwinian than Lamarckian, but we are not. So my theory, like many another of even greater plausibility, but ill stands hard wear. Even in England there are men who see other factors in evolution than natural selection, and to tell the truth these men in the minority are after all the truer upholders of scientific patriotism, for like them Darwin also saw

other agents than selection that made for modification and descent. And so my theory, perhaps, wears quite through and should go to the rag-bag.

The latest conspicuous exposition of the English neo-Darwinian point of view is that embodied in Professor Poulton's "*Essays on Evolution*" (1908, Oxford). Not that the essays themselves are "latest," for their various dates cover the decade between 1896 and 1906, but they are put out now, with revisions and some additions, as the expression of the distinguished author's present point of view. This is clearly and strongly that of a neo-Darwinian, a thoroughgoing selectionist.

The most important and interesting parts of the book are certainly those in which the author exposes the facts and theories of insect mimicry and uses them for argument. These facts and theories are not only the field in which Professor Poulton is especially at home—a field, indeed, which he practically owns—but are also the field in which lie some of the most potent testimony for the deification of selection. Weismann and other neo-Darwinians have never overlooked the stumbling block to Lamarckians and orthogenesisists that protective resemblance, warning colors and mimicry constitute, but Professor Poulton with his immense resources of personal knowledge in this field makes to the same end, far more effective use of the facts. The least pleasing and, for that matter, least profitable part of the book to its readers is the polemic introduction, far too bitter and personal, discussing "mutation, Mendelism and natural selection." It mars the book.

The essays cover a wide range of subjects: "The age of the earth"; "the definition of species"; "Huxley and selection," in which is maintained the surprising thesis that the great champion of Darwin "was at no time a convinced believer in the theory he protected"; "a remarkable anticipation of modern views on evolution," in which Weismann's arguments against the inheritance of acquired characters are shown to have been in rather full measure advanced by James Cowles Prichard, the English anthropologist, in 1826; "theories of heredity," "theories of evolution," and, most extensively and importantly, the facts and theories of insect mimicry. The exposition of these in the last three chapters and special index, is not only most fascinating and stimulating reading but it will serve until we can have the author's promised more extended treatment

in a future book as the latest authoritative exposition of the subject. The book is completed by an amazing analytical index of eighty-three pages, one sixth of the whole book. No reviewer will ever be able to taunt Professor Poulton with that too familiar, "we regret to note the insufficiency of the index."

Finally an entomologist may be pardoned for "pointing with pride," in connection with this book to the splendid work for evolution and general biology that the insects have achieved, in the tireless and skillful hands of Professor Poulton. They have painted a wonderful picture in colors of the possibilities of adaptation and the marvelous capacity of selection—or some other factor. For the moment selection has all the best of the presumption, but this may depend in considerable measure on its great good fortune in the strength of its champion. There is certainly no gainsaying this strength. Professor Poulton, entrenched in his special field of insect bionomics, is perhaps the most serious antagonist that the neo-Lamareckians have to face.

Of somewhat different point of view, and wholly different type, is the other book of Darwinian upholding, which I have at the moment under my eyes. In 1899 Ludwig Plate of the Berlin Landwirthschaftliche Hochschule delivered an address at the meeting of the Deutsche Zoologische Gesellschaft in Hamburg, which was printed in the proceedings of the society under the title "*Über die Bedeutung des Darwin'schen Selectionsprinzips.*" This address both as spoken and printed attracted much attention and the demand for it induced Professor Plate to expand and reprint it in book form in 1903. The admirable comprehensiveness of the discussion in the new form still further increased the interest and demand, as a result of which we have now a revised and still more expanded third edition of nearly 500 pages (twice the size of the second edition) under the title: "Selectionsprinzip und Probleme der Artbildung," with the subtitle "Ein Handbuch des Darwinismus" (1908, Engelmann, Leipzig). The author in the meantime has been made a professor of zoology in the University of Berlin as well as in the Landwirthschaftliche Hochschule.

Plate is an able friend and defender of selection, but his point of view is not that of Poulton. The Englishman holds rigidly to the neo-Darwinian anti-Lamareckism; the German takes the real standpoint of Darwin, he calls on the inheritance of acquired characters to aid selection in its evolutionary task. He

fight Weismanism in almost all of its aspects: panmixia, germinal selection, *Allmacht* of selection. He resists also any serious encroaching of the mutation theory in the province of species-forming and adaptation. His detailed account and reasoned criticism of De Vries's famous theory are admirable. Isolation, especially those forms of it which may be classified under the general head of "Biologic isolation," is treated *in extenso*. In this connection Plate opposes those statements of Wagner and D. S. Jordan, which claim that new species do not arise, or do so only very rarely, in the same geographic range. He refers to the hundred *Gammarus* species in Lake Baikal, the numerous Cladoceran species of *Bythotrephes* in the Caspian Sea, and the eighty or more chromid kinds in Lake Tanganyika, as examples of nearly related forms that have long inhabited the same limited region and yet among which evolution has steadily gone forward. He discusses the old question of the inheritance of acquired characters in a new way, and those pages in which he explains and justifies his admission of the logical necessity of such an inheritance to explain certain types of adaptation constitute one of the most important parts of the book. His treatment of the Darwinian theory of sexual selection and candid admission of its weaknesses is another admirable instance of the broad-mindedness of this Darwinian champion. Finally his account of the objections to selection and their refutation or recognition as partly valid is simply complete, as is his consideration of the species-forming theories auxiliary to selection.

But this fugue of praise grows monotonous, and yet it is hard to introduce any new measure. Perhaps the sparse scattering of pictures may be criticized as being far too meager if illustration was really needed, and easy reading of the text is a little interfered with by the introduction of date and page references into the lines; but these are trifles. The book is excellent arranged both for logical sequence of presentation and for easy reference to any particular phase or topic of the wide subject treated. Professor Plate's acquaintanceship with the active work now going on along the various lines of evolution study and with the literature of the whole subject is manifestly nearly exhaustive. It is especially pleasant to note his generous recognition of American work.

V. L. K.

PARIS, March, 1909.

